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published in

Experimental Brain Research
2011

DOI (link to publisher)

[10.1007/s00221-011-2846-1](https://doi.org/10.1007/s00221-011-2846-1)

document version

Publisher's PDF, also known as Version of record

[Link to publication in VU Research Portal](#)

citation for published version (APA)

Tijtgat, P., Bennett, S., Savelsbergh, G. J. P., DeClerck, D., & Lenior, M. (2011). To know or not to know: Influence of explicit advance knowledge of occlusion on interceptive actions. *Experimental Brain Research*, 214, 483-490. <https://doi.org/10.1007/s00221-011-2846-1>

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To know or not to know: influence of explicit advance knowledge of occlusion on interceptive actions

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Received: 20 October 2010 / Accepted: 16 August 2011 / Published online: 30 August 2011
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Abstract This study examined how explicit advance knowledge might influence adaptive behavior to visual occlusions. Catching performance and kinematics of good ball catchers were compared between no, early and late occlusion trials. Discrete visual occlusions of 400 ms, occurring early or late in the ball's approach trajectory, were randomly interspersed between no occlusion trials. In one condition, the presence and type of occlusion were announced a priori (expected), whereas in another condition no such information was provided (unexpected). Expectation of occlusion resulted in an adapted limb transport and increased grasping time, whereas in the unexpected condition a higher peak of wrist velocity was evident for all occlusion conditions. The observed different adaptations cannot be explained by trial-by-trial adaptations alone and instead provide evidence for the influence

of explicit advance knowledge in the motor response of interceptive actions.

Keywords Explicit advance knowledge · Interceptive actions · Visual occlusion · Adaptations · Kinematics

Introduction

The human perceptuo-motor system has been shown to adapt to information-based perturbations in a variety of tasks, including repetitive (Woodworth 1899; Vince 1948) and discrete aiming tasks (Keele and Posner 1968; Carlton 1981; Moore 1984; Elliott 1988; Elliott et al. 1995), grasping (Wing et al. 1986; Winges et al. 2003; Fukui and Inui 2006), catching (Whiting et al. 1970, 1973; Whiting and Sharp 1974; Sharp and Whiting 1974, 1975; Lamb and Burwitz 1988; Lacquaniti and Maioli 1989; Mazyn et al. 2007b; Dessing et al. 2009) and hitting (Marinovic et al. 2009; van Soest et al. 2010). Imposing such perturbations in experimental settings influences factors such as movement preparation, as well as underlying control processes that are responsible for adaptations in kinematics as the movement unfolds (Elliott and Lee 1995; van der Kamp et al. 1997; Schenk et al. 2004).

However, while it is clear that the availability of sensory information (e.g., full vision vs. occluded vision) during a trial influences motor behavior, Zelaznik et al. (1983) showed that expectancy regarding the upcoming sensory information is an important source of advance information. Zelaznik et al. found that when trials are received in blocked order and hence there is a clear expectation regarding the sensory information, aiming movements under a full vision condition were performed with a higher spatial accuracy compared to a visual occlusion condition.

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However, this difference decreased when trials were received in random order. The implication is that participants were able to use advance knowledge to plan to take advantage of vision when available. Subsequently, it was confirmed that participants also adopt different movement strategies depending on their advance knowledge. For instance, movement kinematics are consistent with an optimized use of visual feedback when an occlusion is expected, compared to a default strategy when occlusion and no occlusion of vision are equally likely (Jakobson and Goodale 1991; Khan et al. 2002; Hansen et al. 2006). Neural evidence for the influence of advance knowledge has been shown in motor learning (Willingham et al. 2002). Being explicitly aware of a repeating sequence activates additional brain areas in the posterior parietal, superior parietal and dorsal prefrontal cortex.

A somewhat different interpretation of differences between movement kinematics and outcome when trials are performed in blocked compared to random order is necessary if one suggests that the visuomotor system is cognitively impenetrable (Song and Nakayama 2007; Whitwell et al. 2008). As an alternative, these authors attributed differences between blocked-order and random-order reaching and grasping to trial-by-trial adaptations. In a catching task, Dessing et al. (2009) showed that early occlusion (i.e., vision occluded for approximately the initial third of flight time) only had an effect when trials were presented in random order. The lack of effect on movement kinematics when trials were presented in blocked order was suggested to result from trial-by-trial adaptations in the visuomotor gain rather than velocity gain. In other words, because participants tried to catch the ball, they were able to adapt visuomotor gain after the previous trial(s), which proved appropriate for the successive trial(s).

While not intending to refute the possibility of trial-by-trial adaptations in the aforementioned work, it is important to consider that trials performed in blocked order also permit the expression of implicit advance knowledge regarding the upcoming availability of information (Tijtgat et al. 2010). The present study, therefore, compared trials received only in a random order, either with or without explicit advance knowledge (see Button et al. 2002 for a comparable design). In this way, the study was designed to determine the influence of explicit advance knowledge when the possibility of trial-by-trial adaptations was minimized. It was hypothesized that providing explicit advance knowledge regarding an upcoming visual occlusion (i.e., early or late) would enable participants to prepare a response optimized to the available information. Specifically, it was expected that for the transport phase of catching, participants would respond with an earlier movement onset, in combination with an earlier and retreated wrist displacement (Button et al. 2002; Mazyn

et al. 2007b). In the grasping phase, a greater peak hand aperture was expected as this increases the safety margin and thereby the likelihood of making a successful catch. However, no change in the timing of the grasp was predicted as this has previously been shown to be robust against visual occlusion (Mazyn et al. 2007b). In the absence of explicit advance knowledge, it was hypothesized that participants would respond initially with a default control strategy irrespective of the presence and duration of visual occlusion (Jakobson and Goodale 1991; Khan et al. 2002; Hansen et al. 2006; Mazyn et al. 2007b).

Methods

Participants

Twenty male, self-declared right-handed participants (mean age: 22.5 ± 2.2 years) with normal or corrected-to-normal vision gave their written informed consent for the experiment, which was approved by the Ethical Committee of the host University. They had experience in some form of ball sport (i.e., soccer, basketball and volleyball) and obtained a catching score of at least 17 out of 20 balls in a pretest (ball speed: 10.62 m/s).

Task and apparatus

Before each catching trial, participants were asked to stand still in a relaxed position with their feet parallel and the thumb of the right hand holding a switch located on the right thigh. Yellow, mid-pressured tennis balls were launched at a distance of 10 m from the participant's frontal plane by a ball-projection machine (Promatch/Mubo B.V., Gorinchem, The Netherlands) with an average ball speed of 10.62 ± 0.12 m/s, resulting in an average ball flight time of 942 ± 11 ms to the participant's frontal plane. The initial height of the ball machine and launch angle was adjusted so that the balls arrived above the participant's right shoulder with a spatial standard deviation of no more than 13 cm. An optoelectric device was mounted at the exit of the ball machine to detect the time of ball release. To minimize auditory anticipation of the moment of ball release, participants listened to instrumental music played through headphones.

Visual occlusions were achieved with a pair of PLATO liquid-crystal occlusion goggles (Translucent Technologies, Inc., Toronto, Ontario, Canada). The goggles were interfaced with a PC that regulated the duration of the transparent and opaque states of the lenses. For early visual occlusion trials, the goggles were open for the first 200 ms after ball release, then closed for 400 ms and finally open again until the next trial. For late visual occlusion trials, the

goggles were open for the first 600 ms and then closed for the remainder of ball flight (i.e., approximately 350 ms depending on the exact location of the ball–hand contact). The goggles were returned to the open state between each trial. The goggles stayed open for the first 10 trials and the interspersed trials without occlusion. The catching movement with the right arm was tracked with a 3D motion analysis system (Qualisys AB, Gothenburg, Sweden) operating at 240 Hz. Eight infrared cameras were used to register the position of reflective markers that were attached with adhesive tape on the following key locations: shoulder (sulcus intertubercularis of the humerus), elbow (epicondylus lateralis and medialis of the humerus), wrist (processus styloideus of radius and ulna) and hand (phalanx distalis of index and digitus minimus). The switch attached to the lateral side of the participant's right thigh was pressed with the thumb of the catching hand in preparation of each trial. The release of the switch generated an analog signal that provided information of the initiation of the catching movement. A microphone was mounted on the forearm near the participant's wrist and was used to record an audio signal that enabled the moment of ball–hand contact to be derived.¹

Experimental design and procedure

The experimental design consisted of two phases that were received in fixed order. The first phase comprised of blocks of trials in which participants were given advance knowledge about the availability of visual information during ball flight (expected condition). Participants were given a written instruction from an experimenter before each trial on the type of occlusion that could be expected: no occlusion (no), an early occlusion (early) or a late occlusion (late). In the second phase, no explicit advance knowledge was provided (unexpected condition), leaving participants to respond to an occlusion as and when it occurred. Both experimental phases comprised of familiarization trials followed by test trials. During familiarization, participants were required to perform the catching task under randomly assigned early or late visual occlusions until a criterion of 7 successful catches out of 10 was achieved for each occlusion. This criterion was used to insure that each participant was sufficiently familiarized to the experimental condition and was reached at on average 46 trials in the advance knowledge phase and 26 trials in the phase without advance knowledge. Participants then completed 10 trials

with no occlusion, followed by 55 no occlusion trials with 10 early and 10 late occlusion trials randomly interleaved ($N = 85$ test trials); for a similar design see Button et al. (2002).

Apart from differences in prior instruction (i.e., advance knowledge or no advance knowledge) between the two test phases, every trial followed the same procedure. Before the ball was launched, the participant looked at the experimenter. After a signal from the experimenter (i.e., raising of the right-hand thumb), the participant focused his gaze on the ball machine and was aware that a ball would soon be released. Participants were instructed to catch as many balls as possible. Trials in which the experimenter reported that there was a major deviation of the normal flight path (only 1.08% of all trials) were not examined but retaken after each session.

Dependent measures and data analysis

Catching performance was evaluated using the number of successful catches for each occlusion (no/early/late) and each expectancy condition (expected–unexpected). Although we attempted to control for learning within and between experimental phases by providing a familiarization phase, it was decided to further minimize possible learning effects by restricting the kinematical analysis to a specific subset of trials. To this end, we selected the last five trials for each of the expected occlusion conditions and the first five trials for each of the unexpected occlusion conditions. Five no occlusion trials were selected according to a criterion that minimized any potential sequence and/or carry-over effects from a preceding occlusion trial. Specifically, the selected no occlusion trials always preceded an early or a late occlusion trial but could not be preceded by another occlusion trial. The selected trials were subjected to a kinematic analysis, which was completed using proprietary motion analysis software (Visual 3D v4.82.0, C-motion Inc., Gaithersburg, MD, USA). The marker position data were filtered using a second-order recursive low-pass Butterworth filter (cut off at 10 Hz). Subsequently, the following kinematic variables were derived from the time-synchronized analog signals of the optoelectronic trigger, thigh-located switch and microphone, in combination with the 3D coordinates of the markers positioned on the catching arm and hand:

Transport variables:

- Latency time (LT, in ms): time between ball appearance and release of the thigh-located switch (movement onset).
- Movement time (MT, in ms): time between release of the thigh-located switch and ball–hand contact.

¹ If this analog signal failed to detect the moment of ball–hand contact, it was derived from the 3D visual reconstruction of the catching movement in the Qualisys software program. A clearly visible sudden jerky backward movement of the index and thumb marker as a consequence of the ball impact was recognized as the moment of contact (Mazyn et al. 2007a).

- Displacement of the wrist (DxW, in cm): distance between the position of the wrist at movement onset and ball–hand contact in the anterior–posterior axis (X-axis).
- Peak Wrist Velocity (PWV, in m/s): first peak of the wrist velocity during the catching action (the momentary wrist velocity was calculated as the resultant of the velocities in the x-, y- and z-axis).
- Time To Peak Wrist Velocity (T_TO_PWV, in ms): time between movement onset and the moment of peak wrist velocity.

Grasping variables:

- Peak of Hand Aperture (PHA, in cm): maximum linear distance between thumb and index during the unfolding of the catch.²
- Grasping time (GT, in ms): time between maximum hand aperture and ball–hand contact.

Given the likely deviation from normal distribution for near maximal performance (especially for no occlusion trials), Friedman's tests were conducted on the catching performance scores, with Wilcoxon signed-rank post hoc tests (Sidak step-down-adjusted *P* values).

The trials selected for the kinematical analysis were submitted to a linear mixed model (variance components was the selected variance structure) with three fixed factors (expectancy, occlusion and trial number) and a random factor (subject). Significant main and interaction effects of expectancy and occlusion were further analyzed using adjusted least significant differences (LSD) tests ($P < 0.05$).

Results

As expected, having completed the familiarization sessions, 92.65% of all balls were caught in the test phase. However, in spite of the high catching scores, there was a significant effect of occlusion for both expected ($\chi^2_{2,20} = 32.39$, $P < 0.001$) and unexpected ($\chi^2_{2,20} = 15.40$, $P < 0.001$) condition. Participants caught more balls (9.70 out of 10) in trials with no occlusion compared to both early and late occlusion trials (on average 7.8 balls out of 10, $P < 0.005$). There were no significant differences between the expected and the unexpected condition. Importantly, in almost all trials in which the ball was not

caught, there was a clear ball–hand contact, which indicates that gross spatial positioning was well maintained.

Table 1 shows the group means and inter-participant standard deviations of transport and grasping variables. Main and interaction effects of expectancy and occlusion for each variable are also presented. Importantly, no effects of trial number were observed, which implies that the effects of expectancy presented in Table 1 most likely were not due to learning across the experiment.

Expectancy

A main effect of expectancy was observed for DxW, an effect that was superseded by an interaction with occlusion (see below). There was also a main expectancy effect for PWV (see Table 1). Participants had a higher maximal wrist velocity in the unexpected condition ($P < 0.001$) compared to the expected condition. No other main effects of expectancy were found.

Occlusion

All kinematic variables showed a significant main effect of occlusion. Occlusion resulted in adaptations in the transport and grasping phase of the catching movement. These effects are summarized in Table 1. Importantly, however, some of these occlusion effects were superseded by an interaction with expectancy (see below).

Expectancy by occlusion

In the transport phase, a significant interaction effect was found for DxW and T_TO_PWV. The expectation of a late occlusion resulted in ball–hand contact being positioned 3.8 cm further forward compared to an expected no occlusion ($P < 0.001$), while in the unexpected condition, the hand was put forward as if a late occlusion was expected (35 cm), with no significant differences between no and late occlusion trials (see Fig. 1). The expectation of a late occlusion also resulted in an 18 ms shorter T_TO_PWV as compared to an expected no occlusion ($P < 0.005$), whereas T_TO_PWV was the same for both no and late occlusion trials in the unexpected condition.

With respect to the grasp kinematics, the timing of the peak of hand aperture (GT) was characterized by a significant interaction effect between expectancy and occlusion. GT was longer for the early occlusion trials than for no occlusion trials in the expected as well as the unexpected condition ($P < 0.001$). Late occlusion trials, however, differed between expectancy condition ($P < 0.001$), with GT-values that corresponded to early occlusion trials in the expected condition and to no occlusion trials in the unexpected condition.

² For most of the participants, a clear peak near the end of the catch characterized hand aperture. However, 5 participants had a plateau shape or a double peak. PHA was then corrected so that it reflects the start of the grasping phase (i.e., a second peak) at the final closure of the hand.

Table 1 Means and standard deviations (SD) of catching performance together with transport and grasp variables for the three visual occlusions (no/early/late) under the expected and unexpected condition

	Expected			Unexpected			Expectancy \times occlusion		Expectancy		Occlusion	
	No	Early	Late	No	Early	Late	F-value (df)	P	F-value (df)	P	F-value (df)	P
Transport variables												
LT (ms)												
Mean	290	290	300	291	287	298	0.258 (2)	0.773	0.195 (1)	0.659	4.686 (2)	0.010*
SD	50	74	83	71	72	82						
MT (ms)												
Mean	596	605	581	592	607	588	1.025 (2)	0.359	0.091 (1)	0.763	14.773 (2)	0.000***
SD	52	72	79	72	73	83						
DxW (cm)												
Mean	32.71	25.31	36.51	35.37	28.05	35.02	7.443 (2)	0.001**	6.435 (1)	0.011*	118.380 (2)	0.000***
SD	7.46	9.25	8.42	8.54	9.62	8.35						
PWV (m/s)												
Mean	3.05	3.09	3.29	3.27	3.20	3.34	2.455 (2)	0.087	16.283 (1)	0.000***	12.246 (2)	0.000***
SD	0.41	0.68	0.68	0.71	0.73	0.80						
T_TO_PWV (ms)												
Mean	230	197	211	215	204	216	4.321 (2)	0.014*	0.106 (1)	0.745	15.502 (2)	0.000***
SD	66	54	76	57	57	64						
Grasping variables												
PHA (cm)												
Mean	11.95	13.03	12.40	12.11	13.00	12.42	1.646 (2)	0.194	1.268 (1)	0.261	183.045 (2)	0.000***
SD	1.36	1.30	1.27	1.37	1.27	1.33						
GT (ms)												
Mean	42	49	50	43	53	40	12.784 (2)	0.000***	2.376 (1)	0.124	18.639 (2)	0.000***
SD	17	20	17	17	24	15						

Statistical main and interaction effects of occlusion and expectancy condition for every dependent variable

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

Discussion

The aim of the present experiment was to elucidate whether and how the human motor system adapts to visual information of an approaching object that is expectedly or unexpectedly perturbed, early or late during its trajectory. The main findings of this study reveal that the observed adaptations to visual occlusions differed when participants were aware in advance of the impending visual condition (i.e., whether there would be an early, late or no visual occlusion).

In contrast to our predictions, movement onset was not affected by the explicit advance knowledge of an upcoming occlusion. However, during the unfolding of the catching movement, there were significant differences between the expected and unexpected condition, although these mostly depended on the visual information available (i.e., interaction effect, see below). An exception was the slightly higher wrist velocity peak for the unexpected condition compared to expected condition (see also Daum et al.

2007). In the absence of advance knowledge, such an observed adaptive response is suggested to give increased opportunities to overcome an uncertain situation (Tijtgat et al. 2010).

Compared to when no occlusion was expected, peak of the wrist velocity was reached earlier and forward displacement of the wrist (DxW) was increased when it was known in advance (i.e., expected late), or there was uncertainty (i.e., unexpected no and late) that there would be a late occlusion (i.e., goggles would or could be occluded from 600 ms after release until the final catch). A different strategy was evident in early occlusion trials, where a time-buying strategy was evident in the gross motor orientation of the hand, irrespective of advance knowledge. Indeed, when vision was occluded between 200 and 600 ms after release, participants located the wrist earlier and closer to the body, which delayed ball–hand contact and thereby increased the time that the ball was visible toward the end of the trial (Fig. 1, see also the increased MT). Such an adaptive strategy enabled

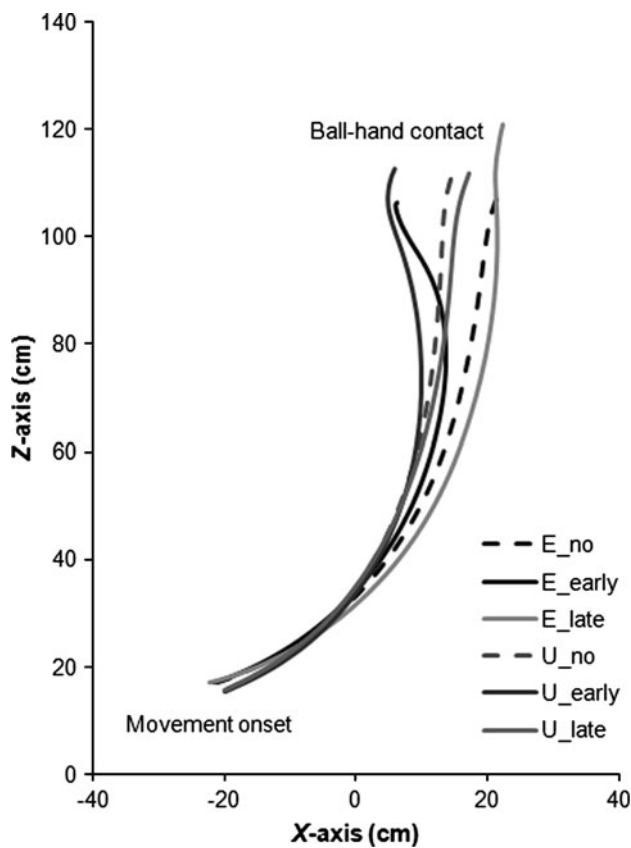


Fig. 1 Mean trajectory of the wrist in the XZ-plane (X-axis represents the anterior–posterior axis and Z-axis the vertical axis) of participant JS for each occlusion (no/early/late) and expectancy (E expected and U unexpected)

participants to take advantage of online control processes and thus minimize any errors that resulted from not having access to vision during the early occlusion.

In the grasping phase, the greater peak hand aperture for occlusion trials corroborates earlier research (Wing et al. 1986; Jakobson and Goodale 1991; Fukui and Inui 2006; Mazyn et al. 2007b; Whitwell et al. 2008; Whitwell and Goodale 2009), which has suggested that increased peak aperture reflects the use of a safety margin when vision is occluded. In the current study, hand aperture was presumably increased in early and late occlusion trials because participants had restricted access to important visual information from ball flight. Differences in grasping time as a function of early occlusions were consistent with those of peak aperture and reflected the increased time needed to close the hand when it was opened wider. Also, an influence of advance knowledge on grasping time was observed for late occlusion trials. Grasping time was longer when a late occlusion was announced a priori. However, when such a late occlusion could not be anticipated, specific adaptations of the timing of the grasp were lacking so that grasping time was equal to trials with no occlusion (see

Table 1). Such adaptations to the grasping phase of catching contrast with previous work that has reported invariant timing across various task constraints (Savelsbergh et al. 1991, 1993; Laurent et al. 1994; Bennett et al. 1999; Mazyn et al. 2006; Tjigtat et al. 2010), as well as in the face of perturbations (Polman et al. 1996; Button et al. 2000; Mazyn et al. 2007b), although it has been previously reported at individual level (Button et al. 2000, 2002).

Taken together, the observed differences between expected and unexpected occlusion trials suggest an influence of explicit advance knowledge on movement execution. This interpretation challenges the suggestion of a visuomotor system that is mainly regulated by trial-by-trial adaptations with only a marginal influence of explicit advance knowledge (de Lussanet et al. 2002; Song and Nakayama 2007; Whitwell et al. 2008, 2009). Notwithstanding the undeniable adaptive process based on previous trials (Scheidt et al. 2001; Zago et al. 2010), it is our contention that explicit (i.e., conscious or declarative) advance knowledge can also exert an influence on the human perceptuo-motor system (Willingham et al. 1989; Willingham 1998). Accordingly, both trial-by-trial adaptations and cognition could affect kinematics on the current trial (Bennett et al. 2010), although this is likely to be influenced by the specific task constraints (i.e., duration and locus of occlusion, nature of eye movements required to track the approaching ball). Indeed, while a common neural network has been identified for procedural and declarative learning, additional brain regions (i.e., posterior parietal, superior parietal and dorsal prefrontal cortex) have been shown to be activated when explicit advance (declarative) knowledge was provided in sequence learning (Willingham et al. 2002).

Summary and implications

This study showed that explicit advance knowledge regarding the upcoming availability of visual information influences the adaptive behavior. Such findings are not consistent with a simple prior history effect (i.e., trial-by-trial adaptation), since this would not predict consistent differences between expectancy conditions. Indeed, in the current study, prior task history was equal for both conditions (randomly assigned occlusion trials). Therefore, the current results add to the call to consider expectancy as an *important constraint on movement systems* (Davids and Button 2000, p. 515). In this way, a tennis players' fast reaction will be affected by the advance knowledge of the opponents preferred shooting direction, just like someone's walking pattern will change when a slippery floor is announced before (see also Marigold and Patla 2002). As such, expectancy should not be disregarded in future experimental methodologies.

Acknowledgments The authors are grateful to Cindy Lowyck and Arnout Sercu for their help in data collection. We also thank two anonymous reviewers for their helpful comments on earlier versions of this paper.

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